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The Influence of Gypsy Moth on the Composition and Nutrient Content of Litter Fall in a Pennsylvania Oak Forest

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ABSTRACT. Litter fall was studied on gypsy moth (*Lymantria dispar* (L.))-defoliated plots and undefoliated plots in a Pennsylvania oak forest. Litter, collected throughout the year, was separated by plant and insect component and analyzed for dry weight and five major nutrients. Total biomass of litter falling on the defoliated and the undefoliated areas was not significantly different. Within the undefoliated plots, 90% of the litter was deposited during the autumn, and tree leaves were the major litter component. Major litter components within the defoliated plots included insect frass, leaf fragments, and tree leaves; 56% of the litter was deposited during the growing season. The nutrient content of litter totaled 73.1 kg/ha on the undefoliated plots, and tree leaves contributed 85% of all nutrients. The nutrient content of litter on the defoliated plots amounted to 94.6 kg/ha; leaf fragments, insect frass, and tree leaves contributed 34, 25, and 29% of all nutrients. Gypsy moth defoliation caused a statistically significant increase in the quantities of N, P, and K and a significant decrease in the quantity of Ca contained in litter fall. These differences are attributed to the gypsy moth altering the composition and seasonal distribution of litter fall. The significance of this nutrient shift is viewed as a further detriment to the health and vigor of host trees. FOREST SCI. 32:855–870.

ADDITIONAL KEY WORDS. Nutrient cycling, (*Lymantria dispar* (L.)).

SINCE ITS introduction in Medford, MA, in 1869, gypsy moth (*Lymantria dispar* (L.)) has plagued forests in the northeastern United States. Originally confined to New England, the insect has in recent years spread through New York, New Jersey, and Pennsylvania, and annual areas of defoliation have reached as high as 5 million hectares. Attempts to keep populations under control in the northeast have proved unsuccessful, and the gypsy moth continues to expand its range to the south and west. With this expansion comes renewed concern about the impact of this insect on forests.

The influence of one or more defoliations on the physiology of host trees and the resulting impact on growth and mortality is well documented (Campbell and Sloan 1977, Ganser et al. 1983, Kulman 1971, Wargo 1981). However, studies on the impact of gypsy moth-caused disturbance on biomass production (other than host trees), energy flow, species composition or dynamics (plant or animal), water, or nutrient cycles are rare or nonexistent. Data that pertain to less obvious but possibly more important and long lasting ecological consequences of heavy insect defoliation must be obtained if the ratio of benefits to costs is to be truly

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maximized by those making pest management decisions (White and Schneeberger 1981).

Because forest systems often attain relatively high levels of productivity on sites too poor for other types of agriculture, it has been suggested that forests have extremely efficient biological nutrient cycles. Forest productivity may actually be more dependent on the rate of organic matter turnover within the forest system than on soil nutrients derived from primary minerals (Tamm 1975).

It has been postulated that phytophagous insects act as regulators of forest primary productivity through their influence on the biological nutrient cycle (Mattson and Addy 1975, Kitchell et al. 1979). Heavy insect defoliation may increase the contribution of nutrient elements in litter fall and thus accelerate the remineralization process (Ovington 1968, Mattson and Addy 1975). This leads to soil enrichment and represents a positive effect of mass defoliator outbreaks. However, quantitative data on the impact of gypsy moth or other defoliators on the forest nutrient cycle are scarce.

A series of experiments was designed to test the hypotheses that gypsy moth defoliation increases the return of nutrients to the forest floor and the rate of remineralization of these nutrients in an upland oak forest in central Pennsylvania (Grace 1979). This paper reports on the impact of heavy gypsy moth-caused defoliation on the seasonal distribution, composition, and nutrient content of litter fall.

METHODS

Study Site

The study area is located in the Bald Eagle State Forest of Centre and Union Counties, PA, which lies in the Ridge and Valley Physiographic Province. Experimental sites were located along a series of adjoining ridges at elevations ranging from 520 to 650 m. Plots were established on lower slopes or benches with slopes of less than 10%.

The area is covered by even-aged, second-growth stands of oak, typical of lower ridge sites of central Pennsylvania (Braun 1967). Overstory trees are generally 60 to 80 years old, and dominants range from 18 to 25 m high and 25 to 50 cm dbh. The number of trees/ha with dbh >10 cm ranged from 520 to 680, and basal area ranged from 25 to 31 M^2/ha. Red oak (*Quercus rubra* L.) and black oak (*Quercus velutina* Lam.) were the most numerous overstory species on the plots, while red maple (*Acer rubrum* L.), white oak (*Quercus alba* L.), chestnut oak (*Quercus prinus* L.), and scarlet oak (*Quercus coccinea* Muenchh.) were also abundant. Yellow poplar (*Liriodendron tulipifera* L.) and black gum (*Nyssa sylvatica* Marsh.) were present infrequently. The closed overstory canopy allowed for a sparse understory with the exception of mountain laurel (*Kalmia latifolia* L.), which was dense in some areas. Other species that occurred sparsely in the understory were red maple, witch hazel (*Hamamelis virginiana* L.), sassafras (*Sassafras albidum* [Nutt.] Nees), and serviceberry (*Amelanchier arborea* [Michx. f.] Fern.). Ground cover was generally lacking, but when present consisted of scattered tree seedlings along with various ericaceous species, primarily *Vaccinium* and *Gaylussacia.*

The soils in the study area are generally of medium to low fertility, less than 125 cm deep, well- to very well-drained, and strongly acidic. All of the soils are derived from either gray or red sandstone, most being residual, stoney sandy loams of the Dekalb and Lehew series, and others are colluvial, stoney loams of the Laidig series.

Climate in the area is characterized by warm summers and rather cold, moderately long winters. The frost-free season generally consists of 150 days and lasts

from early May to the beginning of October. Temperatures in January average −4°C while those of July average 21°C. Annual precipitation averages ca. 100 cm and is evenly distributed throughout the year.

Central Pennsylvania, including the Bald Eagle Forest, was first infested with gypsy moth in the spring of 1973 when ca. 6,000 ha were defoliated. Subsequently, more forests in the region experienced increased amounts of heavy (>60%) defoliation. Aerial surveys carried out by the Pennsylvania Department of Environmental Resources (DER) indicated that the study area received light (0 to 30%) defoliation in 1974. Ground surveys carried out by DER indicated that egg mass densities in the early spring of 1975 ranged from 1,250 to more than 25,000 per ha.

Plot Selection

Because of the heavy infestation of gypsy moth and the potential for severe defoliation, the Pennsylvania Department of Environmental Resources, along with the USDA Forest Service, instigated a number of control operations in the spring of 1975 on the Bald Eagle State Forest. This consisted of aerial spraying with the Thuricide 16B formulation of B.t. (*Bacillus thuringiensis*) and Dylox® 1.5 oil (*Trichlorfon*) in narrow strips along roadways and in blocks surrounding recreational areas. These spray operations protected forest stands from severe defoliation, while adjacent, unprotected stands were heavily defoliated.

A number of stands both within and outside of the sprayed region were chosen for study. Based on visual estimation, the stands were selected to be as homogeneous as possible with respect to species composition, structure, and topographic position. Twelve 20 × 25 m rectangular plots were randomly located within the selected forest stands. Six were in areas where defoliation seemed inevitable due to high egg mass densities, and six in areas where control measures were expected to prevent or greatly limit defoliation. Three litter traps were randomly placed in each of the 12 plots.

Collection Procedure

Litter fall was collected on each plot with three 0.6 × 0.6 m litter traps placed on the forest floor. These traps were constructed of plywood sides, 1.5 cm thick and 20 cm high with a bottom of 18 × 16 mesh fiberglass screen. Samples were taken 18 times between May 1, 1975, and April 30, 1976. During periods of heavy litter fall, the traps were emptied at weekly or more frequent intervals to minimize leaching losses. Traps were emptied at biweekly intervals during the summer and late autumn and only once from December to April, because weather conditions made the area inaccessible.

Branches >2.5 cm in diameter were discarded from all litter traps because the sampling intensity in this study was considered too low for the large amount of variability normally reported for large branch litter (Bray and Gorham 1964). The litter collected from each trap was dried at 80°C, separated into components, and weighed. Litter components included tree leaves by species; other vegetative parts (flowers, fruits, and bud scales); bark; twigs; insect frass; and dead larval carcasses. Subsamples from individual traps were bulked by litter component for each plot by sampling date and ground in a Wiley Mill to pass a #20-mesh sieve. The material was then placed in a sealed, clean glass jar until nutrient analysis was undertaken.

Nutrient Analysis

Nutrient analyses were carried out on bulked litter samples for each major litter component from each of the 12 plots for each sampling period. In cases where a

certain litter component was absent from a plot or an insufficient amount was collected, it was necessary to combine similar components from more than one plot in order to carry out nutrient analysis. During the study, analysis for N, P, K, Ca, and Mg was completed for a total of 642 litter samples. Total nitrogen was determined from 0.5-g samples of the ground, dried litter components by the macro-Kjeldahl procedure (Jackson 1958). The concentrations (% dry wt) of mineral elements P, Ca, K, Mg were determined after dry ashing the samples at 475°C for 6 hours. The ash was dissolved in 20% HCl. Phosphorous concentration was determined colorimetrically using the vanadomolybdophosphoric yellow method (Jackson 1958), and Ca, K, and Mg concentrations were determined by atomic absorption spectrophotometry.

Statistical Treatment

The data for the two treatments (gypsy moth-defoliated and undefoliated) were analyzed as a one-way analysis of variance with subsamples, i.e., nested or hierarchial classification (Snedecor and Cochran 1967). Statistical differences were determined at a significance level of $P = 0.05$.

RESULTS

Biomass

The mean total biomass of litter falling on *undefoliated plots* from May 1, 1975, to April 30, 1976, amounted to 3,586 kg/ha. Tree leaves constituted the major component (Table 1) and accounted for 89% of the total litter. Bark and small twigs amounted to <5% of all litter. Other vegetative parts (e.g., tree flowers and fruits, bud scales, and other deciduous tissues), accounted for <2% of the total.

Sporadic low levels of gypsy moth activity occurred in spite of the control measures, and this resulted in the deposition of small amounts of leaf fragments during the early summer. Likewise, much of the miscellaneous-particle category (e.g., insect frass, leaf fragments, lichens, and other material too small to separate), also resulted from this sporadic defoliator activity. Combined, these components accounted for <5% of all litter.

Total litter deposited on gypsy moth-defoliated plots amounted to 3,439 kg/ha (Table 2). This quantity was not statistically different from the amount returned on the undefoliated plots. Small leaf fragments and frass, which were produced by gypsy moth larvae, accounted for 50% of all litter. These materials began to fall following bud burst of oaks in the latter half of May. They reached a peak during mid-June and ceased in the latter half of July when the gypsy moth pupated.

Following the cessation of insect feeding, notable litter fall ceased for about 1 week. Then as the heavily defoliated oaks began to refoliate, a large quantity of petioles with attached leaf veins fell to the ground. Trees evidently produced an abscission layer at the base of a petiole if 80% or more of its blade was consumed. These veins and petioles continued to fall through July and the first half of August and amounted to 193 kg/ha (6% of the total). Conversely, leaves that retained >20% of their blade remained on the tree until normal leaf fall in the autumn. These partially eaten oak leaves (old oak) had so much of their blades removed that it was impossible to distinguish one species from another.

Small numbers of dead larvae were collected throughout the period of high insect activity (May–June), but the greatest number was collected just prior to pupation (July). The total weight of larval carcasses collected (24.4 kg/ha) was probably underestimated, because the larvae tended to accumulate at the base of trees rather than randomly within the plots.

A second set of foliage (refol. oak) was produced on heavily defoliated oak;

TABLE 1. Mean dry weights (kg/ha) of litter components falling from May 1, 1975 to April 30, 1976 on six undefoliated plots within a Pennsylvania oak forest.

Period	Leaf fragments	Other vegetative parts[a]	Misc. particles[b] ≤4 mm	Tree leaves			Twigs ≤2.5 cm diam.	Bark	Total ± SE
				Oaks	Red maple	Misc. species			
May	0	40.4	2.4	0	0	0	7.4	0	50.2 ± 4
June	27.7	9.6	80.1	12	3	0	13.9	2.5	148.8 ± 34
July–Aug.	9.5	2.4	21.0	20	2	0.6	20.5	0.2	76.2 ± 18
Sept.	0	4.5	4.2	168	28	6.1	17.8	0.9	229.5 ± 19
Oct.	0	1.3	16.0	2,281	594	35.4	21.2	1.2	2,950.1 ± 201
Nov.	0	0	2.0	31	3	0	19.2	0.5	55.7 ± 10
Dec.–Apr.	0	0	2.5	3	0	0	63.7	6.3	75.5 ± 10
Year	37.2	58.2	128.2	2,515	630	42.1	163.7	11.6	3,586 ± 110
±SE	±11.5	±7.6	±36.2	±173	±95	±19.5	±16.4	±2.3	

[a] Fruits, bud scales, tree flowers, other deciduous tissues.

[b] Leaf fragments, insect frass, other small materials.

TABLE 2. Mean dry weights (kg/ha) of litter components falling from May 1, 1975, to April 30, 1976, on six gypsy moth-defoliated plots within a Pennsylvania oak forest.

Period	Frass	Leaf fragments	Dead larvae	Other vegetative parts[a]	Misc. particles[b] ≤4 mm	Tree leaves: Old oak[c]	Tree leaves: Refol. oak[d]	Tree leaves: Red maple	Tree leaves: Misc. species	Twigs ≤2.5 cm diam.	Bark	Total ± SE
May	28	5	0	33.1	3.1	0	0	0	0	7.5	0	76.7 ± 9
June	756	684	8.4	11.9	27.4	0	0	0	0	33.8	0	1,521.5 ± 79
July	40	124	16.0	2.8	7.0	0	0	0	0	7.6	3.1	200.5 ± 14
Aug.	0	105	0	4.5	11.7	16	0	0	0	3.6	0	140.8 ± 26
Sept.	0	0	0	0	12.5	95	0	96	4.6	25.8	4.8	238.7 ± 48
Oct.	0	0	0	2.3	27.1	276	395	417	29.7	12.4	1.0	1,160.5 ± 74
Nov.	0	0	0	0	0.6	3	5	0	1.2	13.0	0.9	23.7 ± 4
Dec.–Apr.	0	0	0	0	2.7	2	0	0	0	62.0	9.9	76.6 ± 10
Year	824	918	24.4	54.6	92.1	392	400	513	35.5	165.7	19.7	3,439 ± 78
±SE	±43	±55	±2.1	±7.4	±9.9	±113	±49	±61	±14.3	±14.3	±4.4	

[a] Fruits, tree flowers, bud scales, and other deciduous tissues.
[b] Leaf fragments, insect frass, and other small materials.
[c] Partially eaten oak leaves that remained on the tree following insect activity.
[d] Refoliated oak leaves.

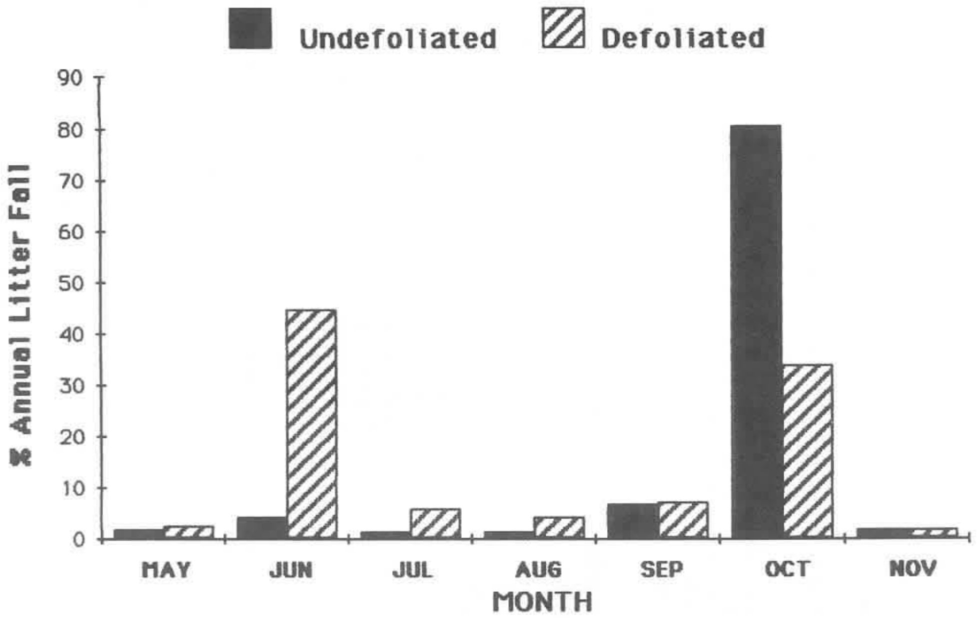

FIGURE 1. Monthly litter fall on gypsy moth-defoliated and undefoliated plots within a Pennsylvania oak forest in 1975.

however, this foliage was extremely sparse in comparison to the foliage on undefoliated trees. The refoliated leaves were smaller than normal and so distorted that species identification was difficult or impossible. The measurement of a random sample of 50 refoliated and 50 normal oak leaves showed that the mean length of the refoliated leaves was 52% of normal, and their mean oven dry weight was only 28% of normal.

Fifty-six percent of the litter on the defoliated plots fell during the growing season (May through August), and 41% was deposited in the autumn (September to November) (Figure 1). In comparison, 90% of the litter on the undefoliated plots was deposited during the autumn, and only 8% was returned during the growing season.

Nutrient Concentrations

Nutrient concentrations varied by litter component and time of deposition (Tables 3 and 4). Concentrations of N, P, K, and Mg were relatively high and Ca relatively low in the litter components that fell during the growing season on both the defoliated and the undefoliated plots when compared to those components that fell during the autumn months. The insect frass and leaf fragments that fell during June, for example, had double the concentrations of N, P, and K, but only about half the concentration of Ca when compared to the leaf litter that fell in October. Concentrations of Mg were less variable and only slightly higher in the litter that fell during the growing season than in the litter returned in the autumn.

Nutrient Return

The total annual litter fall content of the five analyzed macronutrients amounted to 73.1 kg/ha on the undefoliated plots (Table 5). Nitrogen accounted for 43.0% of the total. Calcium (37.3%) was second, followed by K (10.8%), Mg (4.9%), and P (4.0%).

TABLE 3. Mean nutrient concentrations (% dry weight) for litter components that were deposited during periods of greatest litter fall on six undefoliated plots within a Pennsylvania oak forest.

Litter component	N	P	K	Ca	Mg
Leaf fragments (June)	2.51[a]	0.151	0.406	0.50	0.131
Other vegetative parts	2.50	0.139	0.190	0.61	0.102
Misc. particles					
June	1.96 ± 0.15[b]	0.112 ± 0.008	0.386 ± 0.043	0.63 ± 0.05	0.109 ± 0.008
Oct.	1.35	0.094	0.216	0.71	0.102
Leaves					
Red maple (June)	2.02	0.168	0.341	0.51	0.111
Red oak group (June)	2.14	0.150	0.478	0.44	0.119
Red maple (Oct.)	0.74 ± 0.04	0.071 ± 0.006	0.240 ± 0.014	0.88 ± 0.03	0.123 ± 0.006
Red oak group (Oct.)	0.73 ± 0.02	0.079 ± 0.002	0.196 ± 0.015	0.71 ± 0.02	0.096 ± 0.005
White oak (Oct.)	0.75 ± 0.03	0.085 ± 0.010	0.184 ± 0.006	0.84 ± 0.03	0.084 ± 0.004
Chestnut oak (Oct.)	0.75 ± 0.02	0.080 ± 0.005	0.195 ± 0.014	0.89 ± 0.04	0.116 ± 0.013
Misc. species (Oct.)	0.77 ± 0.03	0.076 ± 0.008	0.454 ± 0.020	1.30 ± 0.04	0.232 ± 0.011
Twigs	0.78 ± 0.10	0.057 ± 0.008	0.139 ± 0.028	0.85 ± 0.03	0.059 ± 0.006
Bark	0.93	0.044	0.040	1.85	0.077

[a] N was less than 6 for components that are presented without standard errors.

[b] Standard error of the mean, $n = 6$.

TABLE 4. *Mean nutrient concentrations (% dry weight) for litter components that were deposited during periods of greatest litter fall on six gypsy moth-defoliated plots within a Pennsylvania oak forest.*

Litter component	N	P	K	Ca	Mg
Frass (June)	1.73 ± 0.04[a]	0.106 ± 0.003	0.459 ± 0.007	0.36 ± 0.01	0.136 ± 0.007
Leaf fragments					
Blades (June)	2.44 ± 0.15	0.136 ± 0.002	0.574 ± 0.020	0.30 ± 0.03	0.133 ± 0.006
Veins and petioles (July)	1.55 ± 0.07	0.122 ± 0.005	1.055 ± 0.069	0.61 ± 0.03	0.164 ± 0.012
Larvae	9.60 ± 0.25	0.766 ± 0.043	2.224 ± 0.100	0.12 ± 0.01	0.208 ± 0.014
Other vegetative parts	2.50[b]	0.139	0.190	0.61	0.102
Misc. particles					
June	2.30 ± 0.13	0.119 ± 0.007	0.304 ± 0.022	0.57 ± 0.02	0.102 ± 0.004
Oct.	1.25 ± 0.09	0.115 ± 0.009	0.156 ± 0.015	0.67 ± 0.02	0.131 ± 0.010
Leaves					
Old oak (Oct.)	0.80 ± 0.01	0.076 ± 0.002	0.239 ± 0.021	0.84 ± 0.03	0.109 ± 0.005
Refol. oak (Oct.)	0.89 ± 0.03	0.083 ± 0.004	0.236 ± 0.023	0.78 ± 0.02	0.104 ± 0.007
Red maple (Oct.)	0.70 ± 0.03	0.060 ± 0.004	0.203 ± 0.011	0.83 ± 0.04	0.127 ± 0.011
Misc. species (Oct.)	0.80 ± 0.04	0.070 ± 0.007	0.458 ± 0.028	1.03 ± 0.09	0.307 ± 0.018
Twigs	0.71 ± 0.03	0.050 ± 0.008	0.236 ± 0.040	0.74 ± 0.07	0.048 ± 0.006
Bark	0.75	0.034	0.034	1.96	0.027

[a] Standard error of the mean, $n = 6$.

[b] N was less than 6 for components that are presented without standard errors.

TABLE 5. Mean quantities of nutrients (kg/ha) returned in litter components from May 1, 1975, to April 30, 1976, on six undefoliated plots within a Pennsylvania oak forest.

Litter component	N	P	K	Ca	Mg
Leaf fragments	0.97	0.059	0.12	0.20	0.050
Other vegetative parts	1.46	0.081	0.11	0.36	0.059
Misc. particles	2.42	0.138	0.41	0.82	0.134
Leaves					
Oak species	19.89	2.090	5.33	18.11	2.405
Red maple	4.91	0.427	1.46	5.60	0.778
Misc. species	0.34	0.033	0.18	0.53	0.095
Twigs	1.34	0.082	0.19	1.45	0.087
Bark	0.11	0.005	0.01	0.21	0.009
Total	31.44	2.915	7.85	27.28	3.617
±SE	±1.01	±0.093	±0.46	±0.77	±0.209

Tree leaves of the dominant species were by far the greatest nutrient contributors, returning 85.1% of the total analyzed nutrients (Table 5). Miscellaneous particles contributed 5.4%, and 4.8% of the nutrients were contained in the perennial tissues (twigs and bark). Leaf fragments and other vegetation components returned 1.9% and 2.8% of the total, respectively.

Gypsy moth defoliation caused a significantly greater quantity of nutrients to be returned in litter fall (Table 6). The mean quantity of nutrients contained in the total litter fall on the defoliated plots was 94.6 kg/ha. Nitrogen constituted 55.8% of this quantity followed by Ca (21.0%), K (15.1%), Mg (4.4%), and P (3.7%). The increase in nutrients returned on the defoliated plots was due to statistically significant increases in amounts of N, P, and K, which more than exceeded a significant decrease in the amount of Ca returned. The quantity of Mg returned on the defoliated plots was not statistically different from the amount returned on the undefoliated plots.

Leaf fragments that fell as a result of gypsy moth feeding activity were the greatest nutrient contributors on the defoliated plots, and this component accounted for 33.4% of the total for the five elements analyzed (Table 6). Insect frass contributed 25.4% of all nutrients, and leaves that fell during the autumn comprised 29.2% of the total. Twigs and bark accounted for 3.8%, and larvae, miscellaneous particles, and other vegetation returned 3.2, 2.9, and 2.1% of the total, respectively.

Sixty-seven percent of all the nutrients on the defoliated areas were returned in litter that fell during the growing season compared to only 31% returned in the autumn. In contrast, only 12% of the nutrients on the undefoliated plots were deposited during the growing season, whereas 86% were returned during the autumn. Two percent of the nutrients on both areas were returned in litter that fell during the winter.

DISCUSSION

Biomass

The biomass of annual litter fall on undefoliated and defoliated plots is within the low end of the range of values reported for similar forest types in the eastern

TABLE 6. Mean quantities of nutrients (kg/ha) returned in litter components from May 1, 1975, to April 30, 1976, on six gypsy moth-defoliated plots within a Pennsylvania oak forest.

Litter component	N	P	K	Ca	Mg
Frass	15.19	0.882	3.68	3.16	1.077
Leaf fragments					
Blades	17.29	1.000	4.10	2.34	0.863
Veins and petioles	2.05	0.195	2.22	1.19	0.319
Dead larvae	2.35	0.187	0.54	0.03	0.051
Other vegetative parts	1.37	0.076	0.10	0.33	0.056
Misc. particles	1.80	0.119	0.18	0.57	0.106
Leaves					
Old oak[a]	3.61	0.310	0.98	3.10	0.413
Refol. oak[b]	3.54	0.331	0.90	3.10	0.404
Red maple	3.86	0.327	1.06	3.99	0.664
Misc. species	0.32	0.026	0.16	0.36	0.108
Twigs	1.21	0.077	0.39	1.28	0.077
Bark	0.15	0.007	0.01	0.38	0.005
Total	52.74[c]	3.537[c]	14.32[c]	19.83[c]	4.143
±SE	±1.97	±0.086	±0.64	±0.52	±0.170

[a] Partially eaten leaves that remained on tree following insect activity.
[b] Refoliated oak leaves.
[c] Significantly different from undefoliated, $P = 0.05$, ANOVA (F 1, 10 df).

United States (Bray and Gorham 1964, Cromack and Monk 1975, Gosz et al. 1972, Rochow 1974, Wells et al. 1972).

The results indicate that the total quantity of litter produced during the sampling period was not influenced by heavy gypsy moth defoliation. Rafes (1971), in his study of the influence of an outbreak of gypsy moth on the annual litter fall of a Russian oak forest, also found little difference in the total quantity of litter produced on the defoliated and undefoliated portions of the forest. Similar results were reported for an English oak forest during an outbreak of oak tortrix (*Tortrix viridana* (L.)) (Carlisle et al. 1966).

Alteration in the composition and seasonal distribution of litter fall appear to be the major consequences of gypsy moth defoliation. Unlike the undefoliated areas, where most of the litter was deposited in the form of whole leaves during a short period in the fall, litter fall was bimodal in defoliated plots. The first period of significant litter fall, during the early summer, was a direct result of the heavy gypsy moth feeding. The major litter components deposited during this period were frass and small leaf particles dropped by feeding larvae. The second period was associated with autumnal leaf fall.

The severity of the gypsy moth attack was evidenced by the large amount of frass collected during early summer. The amount of frass on defoliated plots (824 kg/ha) far exceeded the values reported by Gosz et al. (1972) (180 kg/ha), Carlisle et al. (1966) (72 kg/ha), and Reichle et al. (1973) (90 kg/ha) for endemic populations of other hardwood defoliators. Even the outbreak population of *T. viridana* studied by Carlisle et al. (1966) produced only 300 kg/ha of frass. The 300 to 750 kg/ha of frass production reported by Rafes (1971) within a defoliated Russian oak forest is more in agreement with the results of this study.

Leaf fragments, dropped during defoliation, formed the largest litter component

and totaled 918 kg/ha. The quantity of leaf fragments deposited by gypsy moth appears to be very similar to the quantity of frass produced. The ratio of the weight of leaf fragments to insect frass for the six defoliated plots in this study ranged from 0.9 to 1.3, with a mean of 1.1. Rafes (1971) also found that the amount of leaf material added to the forest floor as a result of gypsy moth feeding closely approximated the quantity of frass produced.

The combination of frass, leaf fragments, and other litter components that fell on the defoliated plots from May to August amounted to 1,940 kg/ha and far exceeded the value for the undefoliated plots (276 kg/ha).

The total quantity of leaves removed by gypsy moth larvae may be estimated by comparing the approximate assimilation rate of the feeding insect with the quantities of frass and leaf fragments dropped. The assimilation rates for lepidopterous larvae are generally relatively low, and in many cases may be less than 20% (Petrusewicz and Grodzinski 1975). Moulding (1977) cites an unpublished study by Ahmad and Forgash where the average frass production over the life of a gypsy moth caterpillar fed on fresh oak leaves was 71% of the leaf weight ingested.

Based on this rate, the 824 kg/ha of frass on the defoliated plots represents an ingestion of leaves totaling 1,160 kg/ha. This quantity, plus the 918 kg/ha of leaf fragments dropped by the feeding larvae, gives a figure of 2,078 kg/ha for total leaf removal by gypsy moths. This is equivalent to 83% of the oak foliage and 65% of the foliage for all tree species as determined by the quantity of leaf litter collected in undefoliated stands. Even these figures seemed conservative based on visual estimates. The remaining oak foliage in the gypsy moth-defoliated stands consisted primarily of leaf skeletons, which were barely visible from the ground.

Due primarily to the sparse component of refoliated leaves, the autumnal leaf litter fall on the defoliated plots (1,322 kg/ha) was less than half the amount produced on the undefoliated plots (3,146 kg/ha). Low amounts of autumnal leaf litter in forests that experience large amounts of spring defoliation has been noted in other studies. For example, autumnal leaf litter fall in a Russian oak forest that was 65% defoliated amounted to 1,940 kg/ha as compared to the 3,480 kg/ha of litter returned on the undefoliated control plots (Rafes 1971). Autumnal leaf litter fall on a moderately (30 to 40%) defoliated English oak forest amounted to 1,803 kg/ha as compared to 2,475 kg/ha the following season when no defoliation occurred (Carlisle et al. 1966).

Nutrient Concentration

The relatively high concentrations of N, P, and K and low concentrations of Ca contained in the spring and summer leaf litter closely coincides with the seasonal variation in foliar nutrient concentrations of winter deciduous trees (Guha and Mitchell 1966, Luxmoore et al. 1981, Woodwell 1974). This previous work showed that N, P, and K reach peak concentrations in the leaves during early summer. Once the leaves begin to undergo senescence in late summer or early autumn, a large percentage of these nutrients are translocated from the leaves back into the perennial portions of the plant (Kozlowski 1971). Foliar Mg concentrations in most cases remain relatively stable throughout the year, whereas those of Ca increase during the growing season and reach a peak immediately prior to leaf abscission. Leaf litter falling during the summer returns a greater proportion of the N, P, and K and lower proportions of Ca than does the autumnal leaf litter (Carlisle et al. 1966, Gosz et al. 1972).

The relatively high concentrations of Ca and K contained in the petioles and veins, which were deposited in the summer following defoliation, corroborates the results obtained by Guha and Mitchell (1966). Apparently the petioles of a number of hardwood species have much higher concentrations of Ca and K than the leaf blades.

Nutrient Return

The total quantity of nutrients returned to the forest in litter fall for both the defoliated and undefoliated stands are within the range of values reported for other deciduous forests (Cromack and Monk 1975, Gosz et al. 1972, Peterson and Rolfe 1982, and Rodin and Bazilevich 1967).

Gypsy moth defoliation greatly increased the quantity of N and K returned in litter fall. The return of N on the defoliated plots was 68% greater than on the undefoliated area, and the return of K was 82% greater. Increases of P on gypsy moth-defoliated plots were more moderate (21%), while the return of Ca was 27% lower on the defoliated plots. Even though the return of Mg was 14% greater on the defoliated areas, plot to plot variability was such that this difference was not statistically significant when compared to undefoliated plots.

Although several researchers have suggested that increased quantities of the more mobile elements are returned in the litter fall of forests that experience significant amounts of insect defoliation (Franklin 1970, Mattson and Addy 1975, Reichle et al. 1973), this assumption is supported by little data. Mattson and Addy (1975) cited an unpublished report indicating that heavy defoliation of an aspen forest in Minnesota more than doubled the input of N and P in litter fall. Heavy defoliation of an oak forest in Russia by gypsy moth resulted in increases of 7, 70, 35, and 20% for N, P, K, and Mg, respectively (Rafes 1971). Premature litter fall in a Douglas-fir forest that received a simulated defoliation by tussock moth contained ten times the normal quantity of N and four other nutrients (Klock and Wickman 1978). A reduction in the quantity of Ca contained in litter fall of defoliated forests has not been noted in previous studies.

The increase in the return of mobile elements such as N, P, and K on the defoliated plots occurred primarily because the gypsy moth altered the seasonal distribution of litter fall. Under normal conditions, the greatest amount of leaf litter is deposited in the autumn after much of the N, P, and K has been translocated back into perennial tissues. Gypsy moth feeding causes a large percentage of the leaf litter to drop in the early summer when concentrations of these elements are high. Thus the total quantity of returned nutrients is unusually high in gypsy moth-defoliated areas.

Summer defoliation has the opposite effect on elements such as Ca, which tends to accumulate in leaf tissues throughout the growing season right up to leaf abscission. Because the concentrations are lower in the summer than in the autumn, premature litter fall caused by the gypsy moth results in a decrease in the total quantity returned.

Concentrations of Mg are much more stable throughout the year, and only a small proportion is translocated back into perennial tissues at the end of the growing season. Premature litter fall, therefore, has a smaller effect on the total quantity of Mg returned.

Only five macronutrients were examined in this study, but other nutrients are probably affected in a similar manner. Sulfur, for example, is a mobile element that behaves similarly to N, P, and K (Epstein 1972), and summer defoliation would also increase its return in litter fall. Elements such as Na, Si, Pb, Zn, Ba, B, and Sr are relatively immobile (Epstein 1972, Gosz et al. 1972), and summer defoliation would likely affect them in a manner similar to Ca.

The gypsy moth is not unique in its ability to increase the restitution of certain elements or decrease the return of others. Any disturbance that creates a substantial amount of leaf litter in the spring or summer months would have a similar effect. Gosz et al. (1972), for example, reported that a hailstorm that occurred during the summer caused abundant litter fall, which increased the return of N, P, and K and decreased the return of Ca, Na, and Zn.

Ecological Significance

The increased quantity of nutrients returned to the forest floor in litter fall has been viewed by some researchers as a beneficial aspect of insect defoliation (Mattson and Addy 1975, Rafes 1971). Presumably, the return of a larger quantity of nutrients to the forest floor as a result of defoliation increases soil fertility, which ultimately increases plant production. This accelerated nutrient return is viewed as a protective reaction that helps a forest ecosystem counteract the losses in productivity that result from intense defoliator activity.

However, the results of this study indicate that the increased quantities of nutrients that return to the forest floor as a result of defoliation are relatively modest. For example, in the case of N and P, which are generally the most limiting nutrients in forest ecosystems, the gypsy moth-caused increases (N—21 kg/ha and P—0.62 kg/ha) are quite small compared to typical fertilizer application rates, which range from 170 to 340 kg/ha for N and 50 to 100 kg/ha for P (Auchmoody and Filip 1973). Furthermore, the increased return of nutrients brought about by defoliation is temporarily in organic form and thus may not be available to plants for a year or more.

Although the increased nutrient return will ultimately benefit defoliated forests, these increases occur at the expense of nutrients that are typically stored within the perennial tissues of host trees. Insect defoliators do not import nutrients into infested areas—they merely cause a shift in the nutrient capital of the forest ecosystem from perennial plant tissue to the forest floor.

A large portion of the nutrients lost by host plants is normally used the following spring for shoot growth and leaf production. Therefore, uptake of these nutrients by host trees the following spring has to be significantly increased if the losses are to be rectified and normal growth is to occur. The loss of growth experienced by severely defoliated trees and their increased susceptibility to invasion by secondary agents may be at least partially due to this loss of nutrients.

The increased availability of soil nutrients may serve as a benefit to host trees that recover from defoliation if gypsy moth activity subsides following a single defoliation and environmental conditions are favorable for growth during the years immediately following insect attack. In partially defoliated stands, species that escape defoliation due to their less preferred status (i.e., yellow poplar, maple, or ericaceous shrubs) would likely benefit most from the increased nutrient availability.

The potential benefit to stands that receive two or three successive defoliations would likely be much less. In these stands one could speculate that litter fall would gradually decrease as host trees exhaust their supply of stored food and nutrients following the repeated defoliations. In comparison to undefoliated stands, one would suspect that nutrients returned in litter fall might actually be less in the stands following a second or third year of defoliation. In the long run, this relatively modest nutrient increase is not likely to compensate for the lost productivity resulting from a severe outbreak of gypsy moth. Nevertheless, the increased quantity of nutrients in the soil layer could be expected to benefit regeneration following the mortality of overstory trees.

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